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Changes in snowmelt date and summer precipitation affect the flowering phenology of *Erythronium grandiflorum* (glacier lily; Liliaceae)[1]

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- *Premise of the study*: Climate change has affected species worldwide, including alterations in phenology, migration patterns, distribution, and survival. Because *Erythronium grandiflorum* is an early-season bloomer, alterations in its phenology may have serious implications for many North American Rocky Mountain communities, including changes in resource availability for pollinators and herbivores.
- *Methods*: We investigated whether changes in the snowmelt date, summer temperature, and summer precipitation have altered the timing and abundance of flowering in *E. grandiflorum* by collecting long-term data on floral abundance from 1975–2008 in a series of 2 × 2 m plots at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado in the United States.
- *Key results:* Snowmelt date and mean summer temperature were negatively correlated. Over the 30-yr study, the snowmelt date advanced by 4.14 d/decade, and mean summer temperature increased by 0.38°C/decade. Summer precipitation was variable, showing no change. The first, peak, and last flowering dates of *E. grandiflorum* advanced an average of 3.2 d/decade. Furthermore, earlier snowmelt and greater summer precipitation in the previous year led to earlier flowering in *E. grandiflorum*. There was no change in flowering abundance in this species, indicating it may be controlled by a complex set of abiotic and biotic variables.
- *Conclusions*: Our study indicates that snowmelt is arriving earlier at the RMBL, which has caused earlier flowering in *E. grandiflorum*. Because alterations in phenology can disrupt important ecological interactions, information on potential phenological shifts in species that interact with *E. grandiflorum* is essential in determining the net effect of climate-driven alterations in phenology.

Key words: climate change; *Erythronium*; flowering phenology; glacier lily; Liliaceae; precipitation; Rocky Mountain Biological Laboratory; snowmelt date.

Climate is a major factor controlling the distribution of species (Grinnell, 1917; MacArthur, 1972) because abiotic thresholds determine the abundance and geographic boundaries of species along environmental gradients. Furthermore, there is irrefutable evidence that the Earth's climate is changing due to anthropogenic effects, as reflected by an increase in global average temperature as well as an increase in the frequency of both drought and heavy precipitation events (IPCC, 2007; Knapp et al., 2008). In addition to altered temperature and precipitation regimes, the extent of glaciers and snowpack in montane regions has declined (IPCC, 2007). Due to the link between climate and species distributions, recent reviews and meta-analyses indicate that global climate change has affected species worldwide (Parmesan and Yohe, 2003; Root et al., 2003; Parmesan, 2006; IPCC, 2007), including alterations in phenology, migration patterns, distribution, and survival.

Montane communities may be exceptionally sensitive to changes in climate, due to their occurrence at high elevations, exposure to low temperatures, short growing season, and range-restricted boundaries (McDonald and Brown, 1992; Parmesan, 2006; Hülber et al., 2010). Range-limited species are among the first to become extinct due to recent climate change (Parmesan, 2006). Alterations to the snow–albedo feedback may also exacerbate the effects of warming at higher altitudes (Harte et al., 1995) due to decreases in the extent of glaciers and snow cover. Last, climate change will likely increase the susceptibility of montane communities to biological invasions from lower altitudes (Harte et al., 1995). Due to the potential sensitivity of montane communities to climate change, it is extremely important to determine how these communities respond to changes in climate.

Many species respond to climate change via alterations in phenology (Easterling et al., 2000; Cleland et al., 2007; IPCC, 2007). Spring events such as leaf bud burst and flowering are earlier in many locations, and this earliness has been attributed to warmer temperatures and earlier snowmelt (IPCC, 2007; Cleland et al., 2007). Despite the general trend toward earlier

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plant phenologies, not all species are changing at the same rate. For example in Concord, Massachusetts, rough-stemmed goldenrod (*Solidago rugosa*) is flowering about 11 d earlier for each 1°C increase in temperature (winter and spring), whereas the flowering times of several other species, such as lance-leaved goldenrod (*Euthamia graminifolia*), are not correlated with temperature (Miller-Rushing and Primack, 2008). At our study site in Colorado, we also found that wildflower species such as dwarf and tall bluebells (*Mertensia fusiformis* and *M. ciliata*, respectively), differ in their phenological responses to environmental change (Miller-Rushing and Inouye, 2009; Forrest et al., 2010). Changes in the timing of seasonal activities can affect species growth, reproduction, survival, and distribution (Price and Waser, 1998; Morin et al., 2007; Inouye, 2008). For angiosperms, flowering phenology is a crucial factor determining the number of potential mates (Bronstein et al., 1990), and changes in the timing of flowering can influence recruitment via sexual reproduction (Price and Waser, 1998).

Based on studies to date, the timing of snowmelt is a primary determinant of flowering time in montane plant species (Inouye and McGuire, 1991; Price and Waser, 1998; Inouye et al., 2002, 2003; Dunne et al., 2003; Saavedra et al., 2003; Miller-Rushing and Inouye, 2009; Forrest et al., 2010), especially for early-flowering species (Price and Waser, 1998; Dunne et al., 2003). In addition, the timing of snowmelt can affect flowering abundance for some species (Inouye and McGuire, 1991; Inouye et al., 2002, 2003; Inouye, 2008). Changes in precipitation (Firmage and Cole, 1988; Inouye et al., 2003) and temperature (Inouye et al., 2000, 2003) can also influence the timing and abundance of flowering in montane habitats. Surprisingly, few studies have examined the link between climate and the abundance of flowers, despite its clear importance for reproduction. Examining this link for *E. grandiflorum* may be of particular importance because it is one of the first species to flower in the spring, and alterations in flowering abundance may affect resource availability for pollinators and herbivores.

The goal of this study was to determine whether climatic variables, including snowmelt date, summer precipitation, and temperature, affect the flowering phenology and abundance of *Erythronium grandiflorum* Pursh (glacier lily; Liliaceae). Potential alterations in the flowering phenology and abundance of *E. grandiflorum* may have serious implications for montane communities in the North American Rocky Mountains because it is one of the first species to flower after snowmelt (Inouye et al., 1991; Yamagishi et al., 2005). It is one of very few nectar resources for many pollinators early in the growing season, such as newly emerged bumblebee queens and newly arrived migratory broad-tailed hummingbirds (Inouye et al., 1991). It is also among the first green vegetation for many herbivores, including mule deer recently arrived from lower-altitude wintering grounds (D. W. Inouye, personal observation), and its bulbs are an important resource for grizzly bears (Tardiff and Stanford, 1998). Furthermore, *E. grandiflorum* is both locally abundant at our study site and widespread in the Rocky Mountains (USDA, NRCS, 2008). On the basis of previous studies on the flowering phenology of montane wildflowers (Inouye and McGuire, 1991; Price and Waser, 1998; Inouye et al., 2002, 2003; Dunne et al., 2003; Saavedra et al., 2003), we hypothesized that an earlier snowmelt date, warmer summer temperature, and greater summer precipitation of the previous year would lead to earlier flowering times and lower flower abundance in *E. grandiflorum*.

MATERIALS AND METHODS

Study species—*Erythronium grandiflorum* is a long-lived, herbaceous perennial that often emerges on moist edges of receding snow banks in the central Rocky Mountains of North America (Germino and Smith, 2001; Yamagishi et al., 2005). The distribution of *E. grandiflorum* ranges from British Columbia to New Mexico and from California to Colorado (USDA, NRCS, 2008). Plant growth is initiated in early spring under the snowpack, possibly in response to light penetration through the snowpack (Richardson and Salisbury, 1977). It flowers soon after snowmelt; at our study site, it flowered an average of 8.25 d after snowmelt from 1975 to 2008. An individual flower is typically open for a maximum of 7 d. It is self-compatible, but produces more seeds from outcrossed pollen (Rigney et al., 1993). Vegetative reproduction occasionally occurs by splitting of the corm, but this species does not form clonal patches like some other *Erythronium* species (J. D. Thomson, University of Toronto, personal communication).

Study site—Long-term data on flowering phenology and floral abundance in the West Elk Mountains were collected from 1975 to 2008 in a series of 2 × 2 m plots located at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (38°57.5′N, 106°59.3′W, 2900 m a.s.l.). Plots were randomly selected along an elevation gradient (2864–2973 m a.s.l., well below treeline) in both dry rocky meadow and wet meadow habitats comprised of native vegetation that has not been manipulated (except for the removal of *Veratrum tenuipetalum* plants from one plot in 1974). *Erythronium grandiflorum* occurred in five plots located in both dry rocky meadow (two plots: Rocky Meadow plot 4, Aspen Forest plot 8; close to a temporary stream) and wet meadow (three plots: *Erythronium* Meadow plots 1 and 2, *Veratrum* Removal plot 1) habitats. An aerial photo of the plot locations is shown in Fig. 1 of Inouye (2008) (the lowest and highest plots indicated in the figure). Data were not collected in 1978 and 1990.

Data collection—Approximately every other day during the growing season, from late May to early September, the number of flowering plants, the number of open flowers per plant, and the number of flowering stalks per plant were recorded in each plot. Data on flowering abundance were summed across all plots for each observation date and used to determine first flowering date, peak flowering date, last flowering date, peak number of flowers, number of flowers per stalk at peak flowering time, and flowering duration of *E. grandiflorum* for each year. Before determining flowering phenology variables, data were transformed to days after the vernal equinox. Because the calendar date of the vernal equinox arrives earlier over time until it is reset at the end of most centuries, calculations using day of year may be biased up to 10% of the magnitude of the trend (Sagarin, 2001). First flower date and peak flower date were also calculated in terms of days after snowmelt because snowmelt strongly influences the date of flowering for many species in this habitat (Inouye and McGuire, 1991; Price and Waser, 1998; Inouye et al., 2002; Dunne et al., 2003; Saavedra et al., 2003). Metadata for this project, including GPS coordinates for plots and data collection methods, are accessible from the RMBL website (http://www.rmbl.org) and Digital Repository at the University of Maryland.

Temperature and precipitation data were obtained from the Crested Butte NOAA weather station, located approximately 9.5 km from the study site (2704 m a.s.l.). Data for this station are available from the National Climatic Data Center (http://www.ncdc.noaa.gov). Temperature data were missing for some months from 1977 to 1979. Snowpack data were collected at the RMBL by b. barr from 1975 to 2008 at a site within 1 km of the study plots; snowmelt at that site typically occurs within a few days of snowmelt at the study plots (D.W. Inouye, personal observation). Using these climatic data, we calculated mean monthly temperatures from May to June, monthly precipitation from May to August, and the day of snowmelt for each year. For our analyses, we used mean summer temperature data from May to June, because these months influence the flowering of *E. grandiflorum* in a given year; snow typically melts in April or May, and *E. grandiflorum* typically flowers in May or June. We also calculated the number of growing degree days (GDD) for each day from the snowmelt date to the first flowering date of each year and summed the number of GDD from snowmelt to flowering. We used the following formula: GDD = ([maximum temperature + minimum temperature]/2) − base temperature, where the base temperature was 0°C. We used a base of 0°C because *E. grandiflorum* grows along snowbank edges (Germino and Smith, 2001; Yamagishi et al., 2005) and develops immediately following snowmelt, even in relatively cold temperatures (D.W. Inouye, personal observation). Plants will sometimes grow through the remaining snowpack in the spring.

Statistical analysis—Linear regression analyses (LIN REG, SAS Institute, Cary, North Carolina, USA) were conducted with year as the explanatory variable to determine whether climate variables such as temperature, summer precipitation and snowmelt date, and flowering phenology variables including timing of flowering, peak number of flowers, number of flowers per stalk at peak flowering, and flowering duration of *E. grandiflorum* changed over time from 1975 to 2008. For the temperature data, we also ran linear regression (LIN REG, SAS Institute, Cary, North Carolina, USA) to determine whether temperature changed over time from 1956 to 2005, to have estimates that were directly comparable to the IPCC report (IPCC, 2007). Linear regression analyses (LIN REG, SAS Institute, Cary, North Carolina, USA) were also used to determine whether the number of GDD required for flowering (number of GDD between snowmelt date and first or peak flowering date) varied in response to the snowmelt date. We also conducted a two-sample *t* test, assuming equal variances, comparing the peak number of flowers between years with and without a late frost the previous year (late frosts typically occur in late May or early to mid June). Fruit production is very low in years with late frosts due to frost damage to developing fruits (D. W. Inouye, personal observation). We obtained data on late frosts from an ongoing survey of *Helianthella quinquenervis* demography at the RMBL (Inouye, 2008); flower buds of this species are very sensitive to frost.

We performed multiple regression analyses (PROC REG, SAS Institute, Cary, North Carolina, USA) to determine whether flowering phenology variables such as first flowering date, peak flowering date, peak number of flowers, number of flowers per stalk at peak flowering, and flowering duration were related to climatic variables including mean summer temperature, summer precipitation in the previous year, snowmelt date, and peak number of flowers in the previous year. Climate variables were treated as the explanatory variables, and phenology variables were treated as the response variables. To ensure there was no collinearity among explanatory variables in the multiple regression analysis, we ran a correlation analysis (PROC CORR, SAS Institute, Cary, North Carolina, USA) and calculated Pearson correlation coefficients for each pair of explanatory variables. Snowmelt date and temperature were highly negatively correlated ($r = -0.723$, $P < 0.001$). Thus, two separate multiple regression models (one containing snowmelt date and one containing temperature) were generated; the best model was selected using the Akaike information criterion (AIC) (Akaike, 1973). Based on lowest AIC values, the multiple regression model containing snowmelt date, as opposed to summer temperature, is reported.

RESULTS

Flowering phenology—The mean first flowering date for *E. grandiflorum* from 1975 to 2008 (all five plots) was May 28 ± 1.8 d (±SE), the mean peak flowering date was June 3 ± 1.5 d, and the mean last flowering date was June 10 ± 1.9 d (data presented in graphs as days after vernal equinox). The mean peak flower number (sum of all plots) was 79.3 ± 6.9, and the mean number of flowers per stalk at peak flowering time was 1.26 ± 0.03. The mean flowering duration per plot was 13.3 ± 0.7 d.

Changes in flowering phenology over time—Regression analyses indicated that the first, peak, and last flowering dates of *E. grandiflorum* occurred earlier over time over the 30-year study period. The first flowering date is occurring 4.7 d earlier/decade ($F_{1,32} = 9.76$, $P = 0.004$, $R^2 = 0.234$), the peak flowering date is occurring 2.9 d earlier/decade ($F_{1,32} = 4.56$, $P = 0.041$, $R^2 = 0.125$) and the last flowering date is also occurring 2.9 d earlier/decade ($F_{1,32} = 4.25$, $P = 0.047$, $R^2 = 0.117$) (Fig. 1). The flowering duration is 1.8 d longer/decade ($F_{1,30} = 6.78$, $P = 0.014$, $R^2 = 0.184$). There was no change over time in the number of days between snowmelt date and first flowering date ($P = 0.384$) or peak flowering date ($P = 0.863$). There was also no change over time in the peak number of flowers ($P = 0.973$) or the peak number of flowers per stalk at peak flowering time ($P = 0.145$) in *E. grandiflorum*.

Changes in climate over time—The date of snowmelt was variable and showed a weak, marginally nonsignificant trend toward earlier snowmelt (4.14 d earlier/decade, $F_{1,32} = 2.82$, $P = 0.103$, $R^2 = 0.081$). Mean summer temperature from May to June increased at a rate of 0.38°C/decade from 1975 to 2008 ($F_{1,33} = 9.24$, $P = 0.005$, $R^2 = 0.219$) (Fig. 2). However, when we ran our temperature data for the same time period reported by the IPCC (IPCC, 2007), the mean summer temperature from May to June decreased at a rate of −0.17°C/decade from 1956 to 2005 ($F_{1,48} = 4.21$, $P = 0.045$, $R^2 = 0.08$). There was substantial variation among years in precipitation from May to August (range = 8–27 cm), but no change over time in the amount of summer precipitation ($P = 0.880$).

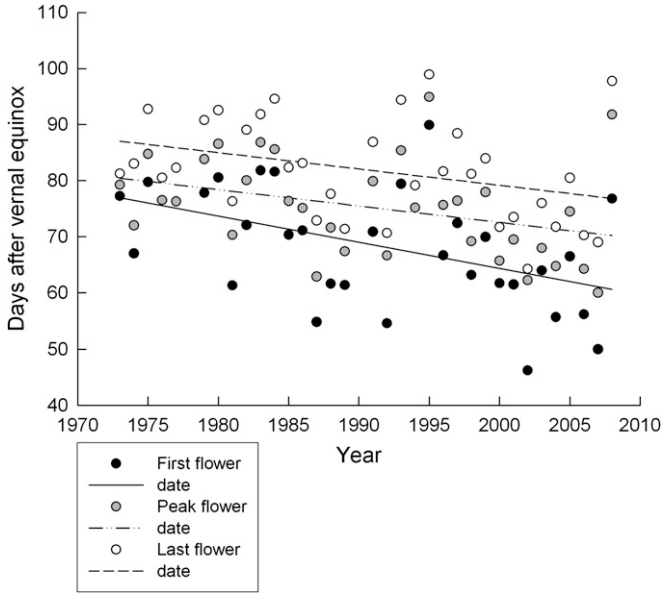

Fig. 1. Linear regression of the change over time in the first flowering date ($F_{1,32} = 9.76$, $P = 0.004$, $R^2 = 0.234$, slope = −0.470), peak flowering date ($F_{1,32} = 4.56$, $P = 0.041$, $R^2 = 0.125$, slope = −0.290), and last flowering date ($F_{1,32} = 4.25$, $P = 0.047$, $R^2 = 0.117$, slope = −0.290) for *E. grandiflorum*.

Relationship between flowering phenology and climate—Multiple regression analyses indicated that the snowmelt date and the amount of summer precipitation in the previous year were significantly related to first and peak flowering dates in *E. grandiflorum*. An earlier snowmelt date ($t_s = 7.03$, $P < 0.001$, slope = 0.537 d/day change in snowmelt) and greater summer precipitation in the previous year ($t_s = -2.16$, $P = 0.040$, slope = −1.168 d/cm) led to an earlier first flowering date (overall model $R^2 = 0.651$) (Fig. 3). Similarly, an earlier snowmelt date ($t_s = 8.48$, $P < 0.001$, slope = 0.497 d/day change in snowmelt date) and greater summer precipitation in the previous year ($t_s = -2.07$, $P = 0.047$, slope = −0.862 d/cm) led to earlier peak flowering dates (overall model $R^2 = 0.724$).

Variation in flowering abundance—Multiple regression analyses also indicated that the peak number of flowers in the previous year explained a statistically significant, but small, portion of the variation in the number of flowers per stalk at peak flowering time ($t_s = -2.24$, $P = 0.038$, slope = −0.0015). When the peak number of flowers in one year was greater, there were fewer flowers per stalk at peak flowering time the following year (overall model $R^2 = 0.174$) (Fig. 4). None of the explanatory variables in the multiple regression analyses explained the peak number of flowers or flowering duration in *E. grandiflorum*.

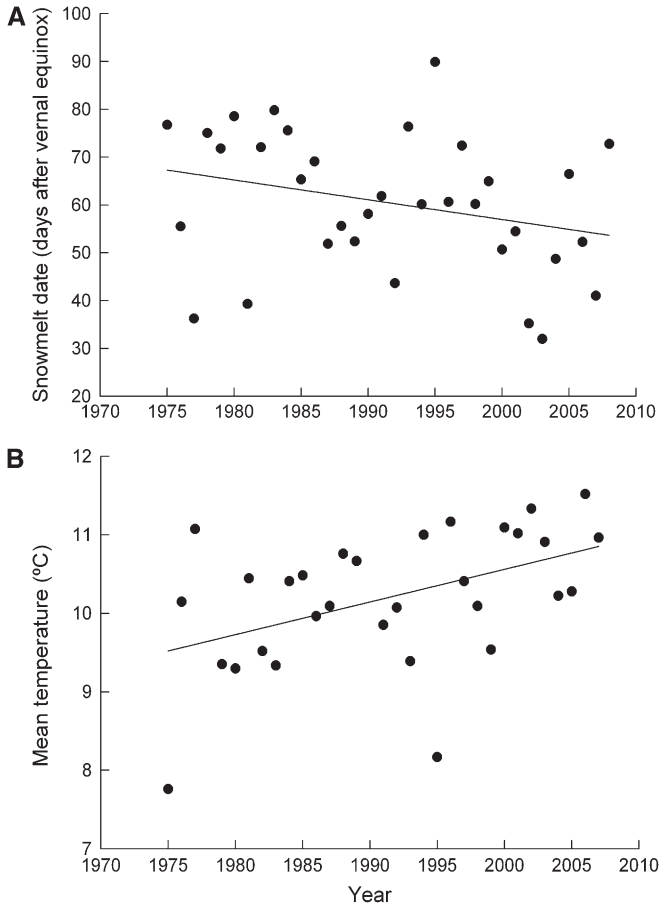

Fig. 2. Linear regression of the change over time in the (A) snowmelt date (days after vernal equinox) (4.14 d earlier/decade, $F_{1,32} = 2.82$, $P = 0.103$, $R^2 = 0.081$, slope = −0.414) and (B) mean temperature (°C, May–June) (0.38°C increase/decade $F_{1,33} = 9.24$, $P = 0.005$, $R^2 = 0.219$, slope = 0.038).

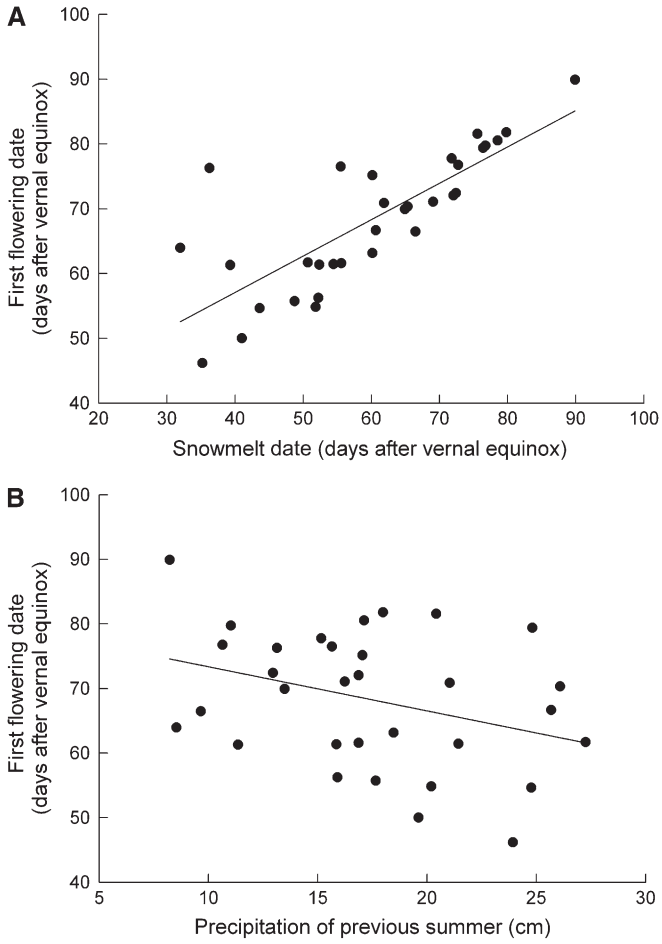

Fig. 3. Relationship between (A) snowmelt date and first flowering date (days after vernal equinox) ($t_s = 7.03$, $P < 0.001$, slope = 0.537 d/day change in snowmelt) and (B) precipitation of the previous summer (cm) and first flower date (days after vernal equinox) ($t_s = -2.16$, $P = 0.040$, slope = −1.168 d/cm) for *E. grandiflorum* (overall model $R^2 = 0.651$).

However, when we compared the peak number of flowers between years with and without a late frost the previous year, we found the peak number of flowers was greater in years where no frost damage occurred the previous year ($t_s = 2.20$, $P = 0.0317$, $df = 29$).

Relationship between GDD and timing of flowering—Linear regression analyses also indicated that the snowmelt date explained a significant amount of the variation in the number of GDD between snowmelt date and the first and peak flowering dates. There was a negative relationship between snowmelt date and the number of GDD between snowmelt and the first flowering date ($F_{1,28} = 15.70$, $P < 0.001$, $R^2 = 0.360$, slope = −2.48 GDD/day change in snowmelt date) and peak flowering date ($F_{1,28} = 50.48$, $P < 0.001$, $R^2 = 0.643$, slope = −2.89 GDD/day change in snowmelt), where there were a greater number of growing degree days between snowmelt date and flowering date when the snow melted earlier (Fig. 5).

DISCUSSION

Our results indicate that the timing of flowering in *E. grandiflorum* has changed since 1975. *E. grandiflorum* has shifted toward earlier first, peak, and last flowering dates; the average advancement of these three dates is 3.2 d/decade. The flowering advancement we observed in *E. grandiflorum* is slightly greater than other species, as determined by a meta-analysis of phenological shifts for species in the northern hemisphere, which indicated an advancement in phenology of 2.3 d/decade across all species in their analysis (Parmesan and Yohe, 2003). The flowering duration is also lengthening, because the first flowering date is advancing more rapidly than the last flowering date. One possible explanation for the longer flowering duration is that cooler temperatures earlier in the spring may lead to slower development, which may lengthen the flowering time. Although the temperature and snowmelt date were negatively correlated, we expect a greater potential for plant exposure to cold temperatures when the snow melts early. Furthermore, in areas with dry climates, snowmelt date is advancing due to decreased snow cover and increased dust deposition, which darkens the snow and causes it to melt faster (Painter et al., 2007). It is also possible that flowering duration is influenced by changes in the spatial distribution of snowmelt or pollination patterns. If the snowmelt date becomes more variable across elevation and habitat gradients, it may lead to longer flowering durations. If flower longevity is influenced by pollination, and if the trend toward earlier flowering has resulted

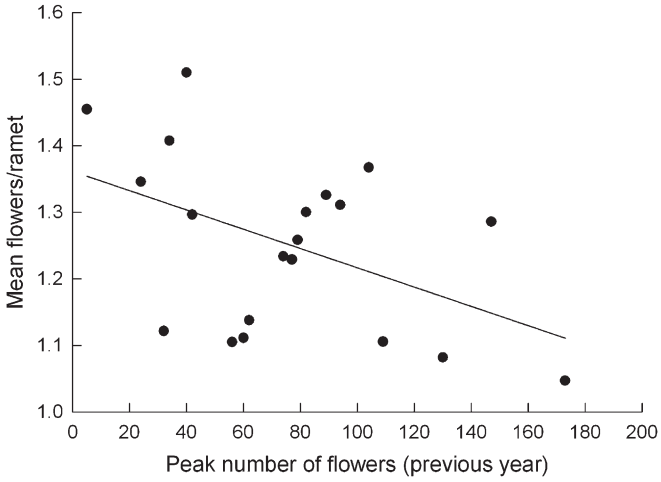

Fig. 4. Relationship between the peak number of flowers (previous year) and the mean number of flowers per ramet (stalk) at peak flowering time ($t_s = -2.24$, $P = 0.038$, slope = −0.0015).

in lower levels of pollination, this may explain the trend for longer flowering duration.

The change in the length and timing of flowering for *E. grandiflorum* has important ecological implications because it may disrupt ecological relationships with species such as pollinators, herbivores, and competitors (Stenseth and Mysterud, 2002; Visser and Both, 2005; Parmesan, 2006). The disruption of ecological interactions can alter the growth, reproduction, and survival of *E. grandiflorum* as well as other species in the community (Memmott et al., 2007). Because it is one of the first species to flower in the spring, newly emerged bumblebee queens and newly arrived migratory hummingbirds may undergo a reduction in resource availability due to the mis-timing of seasonal activities (Inouye et al., 1991). The lengthened flowering period also suggests that relationships with coflowering species may be changing. The overlap in flowering period among species may be increasing or decreasing depending on the relative direction and rate of change in flowering phenology across different members of the community (Price and Waser, 1998; Forrest et al., 2010).

Information on potential phenological shifts in species that interact with *E. grandiflorum* is essential to determine the net effect of climate-driven alterations in phenology. For example, previous analyses of the timing of marmot emergence at our study site indicated that marmot emergence is advancing faster than the timing of snowmelt (Inouye et al., 2000). In contrast, we found that the average advancement in flowering for *E. grandiflorum* is at a slower pace than snowmelt. Thus, as temperatures warm, marmots may have to survive a longer time in the spring between emergence from hibernation and appearance of the first green vegetation, their primary food. Although marmots do not appear to eat *Erythronium* leaves or flowers, the altered phenology of this plant may be indicative of what is happening to plants that marmots do eat (Armitage, 2003). For example, in our study region chipmunks are observed to eat *E. grandiflorum* flowers; these observations occurred very early in the growing season when other resources are scarce (J. D. Thomson, University of Toronto, personal observation).

We also observed changes in climatic variables, including an increase in summer temperature of 0.38°C/decade from 1975 to

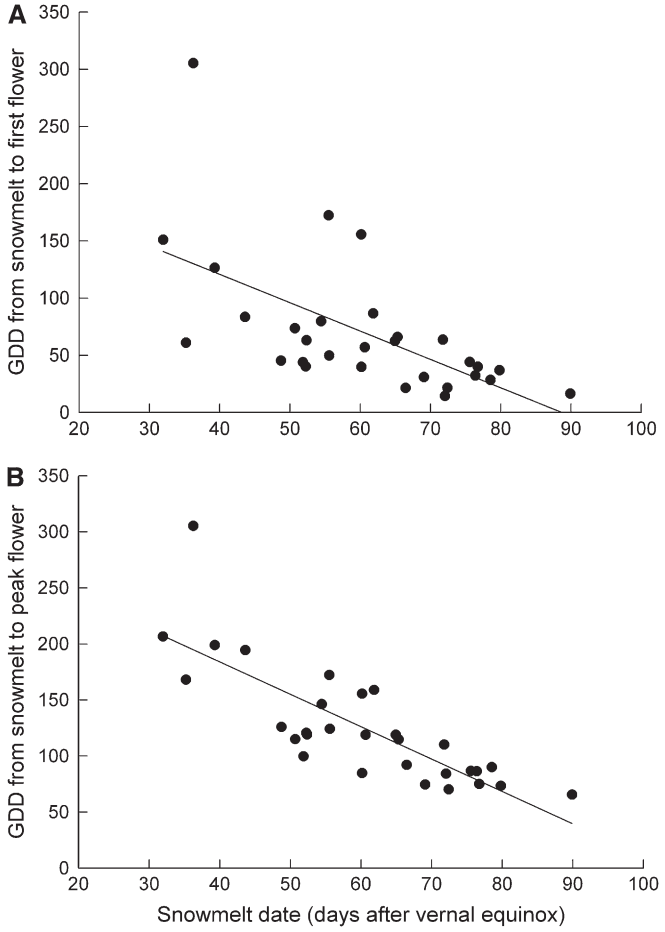

Fig. 5. Relationship between the snowmelt date (days after vernal equinox) and the number of growing degree days (GDD) between snowmelt date and (A) first flowering date (days after vernal equinox) ($F_{1,28} = 15.70$, $P < 0.001$, $R^2 = 0.360$, slope = −2.48) and (B) peak flowering date (days after vernal equinox) ($F_{1,28} = 50.48$, $P < 0.001$, $R^2 = 0.643$, slope = −2.89).

2008. However, when we ran the analyses from 1956 to 2005, the same time period from the IPCC report, we observed a decrease in summer temperature of −0.17°C/decade. Both of these results differ from the global linear warming trend of 0.13°C/decade for the 50 years from 1956 to 2005 (IPCC, 2007). Our results show a slight cooling trend, with a recent warming trend that is expected to increase in the future (Stewart et al., 2004; Seager et al., 2007). Additionally, greater than average warming has been predicted for this region of the Rocky Mountains (IPCC, 2007), which may have strong consequences for species growth and survival.

The shift in *E. grandiflorum* toward earlier flowering may indicate its ability to acclimate to changing environmental conditions such as global climate change (Willis et al., 2008). Indeed, our results indicate that variation in climatic variables including snowmelt date and summer precipitation influenced the flowering phenology of *E. grandiflorum*, where earlier snowmelt and greater summer precipitation the previous year were associated with earlier flowering in *E. grandiflorum*. However, the timing of snowmelt did not affect flower abundance, as it has for other species in this area (Inouye and McGuire, 1991; Inouye et al., 2002; Saavedra et al., 2003).

Our results support previous studies that indicate snowmelt date as a primary factor determining the timing of flowering in montane plant species (Inouye and McGuire, 1991; Price and Waser, 1998; Inouye et al., 2002, 2003; Dunne et al., 2003; Saavedra et al., 2003). Conversely, summer precipitation has not been previously reported to affect flowering phenology the subsequent year, and the causation behind this correlation is not clear. One hypothesis is that increased summer precipitation might benefit growth of the corm, perhaps by increasing the length of time when leaves remain green and photosynthesize, and the increase in stored photosynthate could result in earlier or faster growth during the subsequent season. *Erythronium grandiflorum* is a long-lived perennial that can develop for many years prior to initial flowering, then appears to flower almost every year (O'Callaghan, 1994; D. W. Inouye, personal observation).

Although variation in climatic variables affected the timing of flowering in *E. grandiflorum*, we did not find any relationships between our selected climate variables and flowering abundance. For several other species of wildflowers in the same habitats, flowering abundance is related to climatic variation (Inouye and McGuire, 1991; Inouye et al., 2002, 2003; Inouye, 2008; Miller-Rushing and Inouye, 2009). However, in some instances flower abundance appears to vary independently of climate (Inouye et al., 2003). It is possible that flower abundance in these climate-independent species is controlled by other abiotic variables such as nutrient availability, photoperiod, or the severity of winter temperatures. Biotic factors such as the previous year's growth or fruit set (i.e., a cost of reproduction) and developmental events during late summer or autumn months may also influence flowering abundance. A study of individual plants, rather than the plot-wide scale of this study, would clarify these relationships. Previous work with tagged *Erythronium* plants near RMBL showed a negative correlation between fruit production one year and probability of flowering the next year (O'Callaghan, 1994).

We found that the peak number of flowers in a given year explained the number of flowers per stalk at peak flowering time the following year, such that a greater peak number of flowers in a given year was associated with a lower number of flowers per stalk at peak flowering the next year. This finding supports a previous study of the same species near RMBL indicating that there is a cost of reproduction (O'Callaghan, 1994), which is not surprising because the fruits and seeds are relatively large compared to leaf size. In contrast, we also found that the peak number of flowers was greater in years where no frost damage occurred the previous year. This result is contrary to expectation, where one would expect greater flowering production in years where frost damage occurred the previous year, due to saved resources not spent on reproduction. However, if the photosynthetic structures are also damaged by frost, corm growth may be limited by reduced photosynthetic capacity, which could limit the resources available for reproduction the following year. Clearly, other factors also govern flower production in this species. Although we found that the peak number of flowers in a given year explained the number of flowers per stalk at peak flowering the following year, it is intriguing that we did not find a similar negative relationship between peak number of flowers in one year and the peak number of flowers in the next year. The lack of relationship between peak number of flowers in one year and peak number of flowers in the following year suggests the relationship between flower abundance between years is relatively weak, but deserves further investigation at the individual rather than population level.

We also found that the snowmelt date explained variation in the number of GDD between the snowmelt date and both first and peak flowering date, such that a greater number of GDD were needed for flowering when the snow melted earlier, and vice versa. One explanation is that when snowmelt is late, the plants initiate growth under the snow and require less development and a lower number of GDD to flower. Indeed, *E. grandiflorum* often grows along snowbank edges (Germino and Smith, 2001; Yamagishi et al., 2005), and its tolerance of colder temperatures allows it to start development prior to snowmelt. Alternatively, growth may simply proceed at a faster pace following a late snowmelt, suggesting that factors associated with day of year (i.e., daylength) may mediate the effect of temperature on growth rate. Also, the average temperature is warmer when snowmelt is late, which may give plants more consistent favorable growing conditions, in comparison to intermittent frosts and snow that might negatively impact growth of plants in years with early snowmelt.

In conclusion, our results indicate that the flowering phenology of *E. grandiflorum* is shifting in response to changing climate. Flowering in this species is occurring earlier, and the timing is directly related to earlier snowmelt and greater summer precipitation in the previous year. Because *E. grandiflorum* is one of the first species to flower in the spring at the RMBL, often providing the first resource for pollinators and herbivores, these findings may have serious implications for ecological interactions. Future studies should investigate whether the phenologies of species associated with *E. grandiflorum* are also changing in response to climate.

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